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EARLY STAGES IN THE DEVELOPMENT OF THE SPOROPHYTE OF SPHAGNUM SUBSECUNDUM

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In the spring of 1913 while following through the life cycle of Sphagnum in the field the writer was able to find a great wealth of young sporophytic material. In order to make a detailed study several strengths and combinations of chromic and acetic acids were used as fixing agents. However, it was extremely disappointing to find that in every case the young sporophytes were completely plasmolyzed so that an interpretation of sectioned paraffin material was impossible. Time now being an important factor, as a last resort the dissection of the young sporophytes from the venters of the archegonia was undertaken. While the task was a laborious one, it proved to be relatively simple. The archegonia were first dissected from the tips of the branches on which they were growing. Then the basal portion of each venter, or, in the older stages, of the swollen stalk was carefully dissected, using slender needles for the operation. After the venter or the swollen stalk had been opened, gentle pressure on the neck of the archegonium was usually sufficient to cause the young sporophyte to slip out.

More than one hundred young sporophytes were examined. The study and drawings were made from the living material and are illustrative of the general conditions found. While the results confirm in a general way the work of Waldner, there are points of difference which make the publication of these observations seem worth while.

HISTORICAL

In 1858 Schimper[1] first attempted to trace the development of the sporophyte of Sphagnum. He described the first wall as being almost horizontal; then quickly follow radial, vertical, and horizontal walls, so that in a short time the single cell has become a long, many-celled, pear-shaped body. Schimper further thought that only the lower part of the young sporophyte—that which bores its way into the stalk of the archegonium—develops into the mature capsule. The upper portion he believed disintegrated and was resorbed.

In 1887 Waldner[2] studied the details of the development of the sporophyte using chiefly *Sphagnum acutifolium* Ehrh. He states that the egg

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[1] Schimper, W. P. Versuch einer Entwickelungsgeschichte der Torfmoose. Pp. 96, pls. 1–27. Stuttgart, 1858.

[2] Waldner, M. Die Entwickelung der Sporogone von Andreaea und Sphagnum. Pp. 25, pls. 1–4. Leipzig, 1887.

in the venter of an archegonium ready for fertilization is ovoid or somewhat pear-shaped, and shows clearly a nucleolus with a nuclear body (his Taf. II, fig. 1). The fertilized egg is drawn very indefinitely, and no description is given save that it is surrounded by a hyaline mass of slime (Taf. II, fig. 2). The fertilized egg divides transversely, the upper half being the apical cell. A two-celled embryo is drawn in which the upper cell is relatively small as compared with the basal segment. Waldner states that the apical cell, by walls parallel to its base, cuts off a series of segments from 6 to 8 in number. The basal cell makes only a few irregular divisions and does nothing more. Waldner's figures show that the wall separating the basal and apical segments is sharply defined and may be followed for some time in the subsequent stages of development of the young sporophyte.

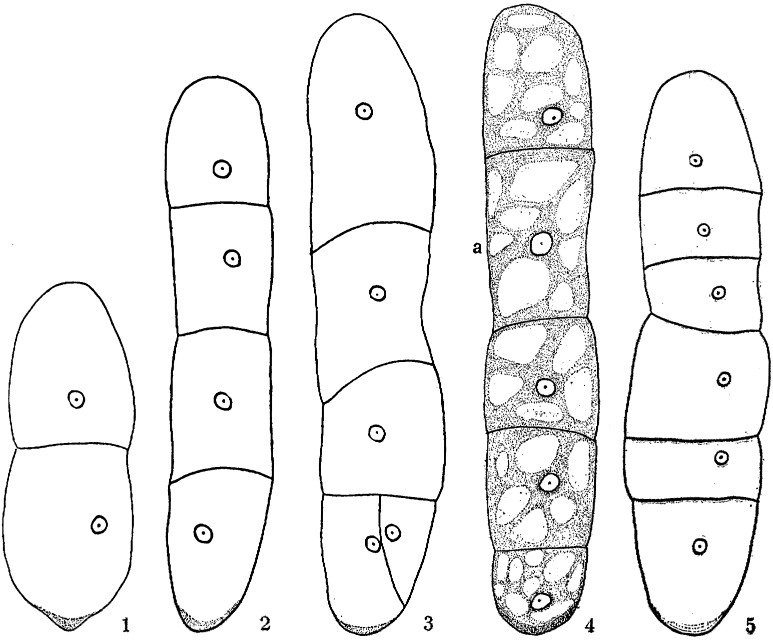

FIG. 1. Embryo of 2 cells. FIG. 2. Embryo of 4 cells. FIG. 3. Embryo of 4 primary segments. Apical cell much elongated, probably preparatory to division. Basal segment has divided irregularly. FIG. 4. Embryo of 5 cells, showing cytoplasmic details at this stage. FIG. 5. Embryo of 6 cells. All × 300.

FERTILIZATION, AND THE DEVELOPMENT OF THE YOUNG SPOROPHYTE

After a number of attempts, fertilization was brought about in the laboratory by squeezing the heads of antheridial plants and immediately allowing the exuding liquid to drop on the tips of archegonial plants which were almost entirely submerged in water. A detailed account of these experiments may be published at some later date. Unfortunately, at the time of fertilization there occurs in the venter of Sphagnum the development of a considerable amount of mucilaginous matter which entirely invests the fertilized egg, and which thus far has proven difficult to penetrate with fixing agents. Since the results are not entirely satisfactory, because of plasmolysis, statements concerning the structure of the fertilized egg will be omitted.

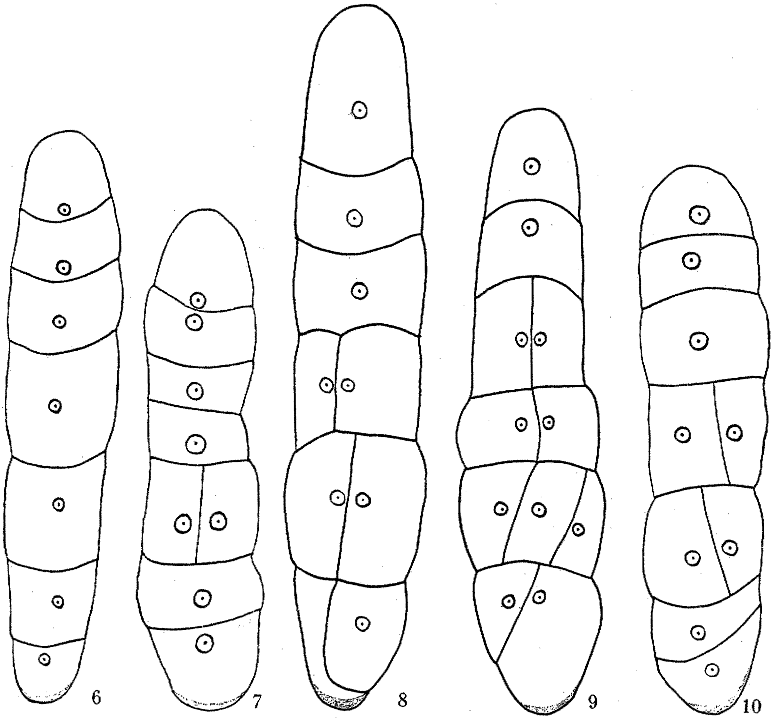

FIG. 6. Embryo of 7 cells. Slender type. FIG. 7. Embryo of 7 primary segments. First vertical wall appears in one segment. FIG. 8. Embryo of 6 primary segments three of which show vertical walls. The two cells of the basal segment are rounding away from each other. FIG. 9. Embryo of 6 primary segments, the basal portion much larger than the apical. FIG. 10. Embryo of 7 primary segments. All × 300.

The first wall is at right angles to the axis of the archegonium and divides the young sporophyte into two approximately equal cells which elongate in the direction of the axis of the archegonium (fig. 1). The basal cell is characterized at its lower extremity by a peculiar greenish zone which is probably related in some fashion to the digesting action of this cell. This zone is clearly visible in all the early stages (figs. 1–15) and serves as a convenient means of distinguishing the basal from the apical end of the embryo when dissected from the venter of the archegonium. After the two-celled stage has been reached there are further divisions by walls parallel to that first formed, resulting in the production of a filament of cells usually six or seven in number before walls make their appearance in other planes (figs. 1–6). Occasionally, as illustrated by figure 3, the basal cell may divide quite early in other than a transverse plane. However, the filament of cells without such irregular divisions is the common occurrence in the material studied at these early stages.

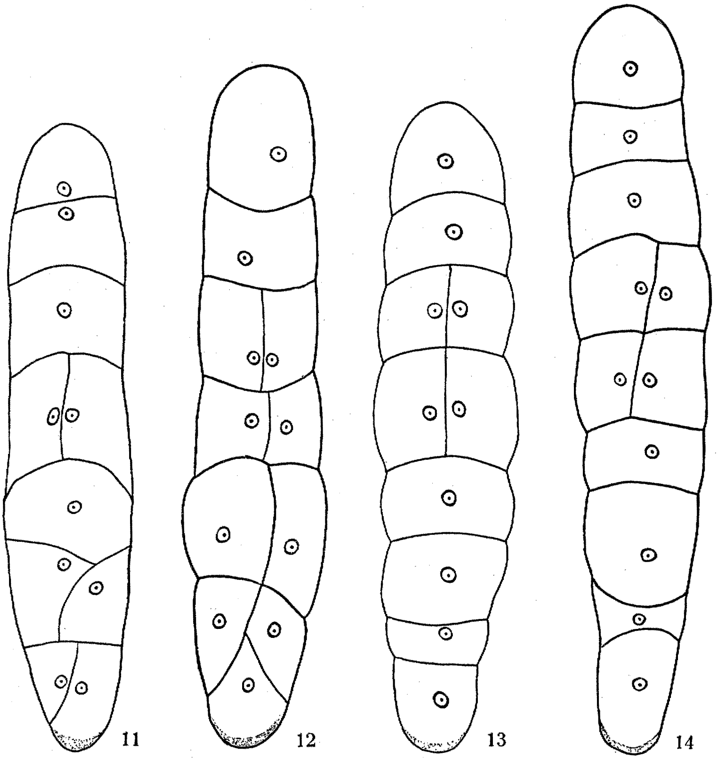

FIG. 11. Embryo of primary segments. Two basal segments show irregular divisions. FIG. 12. Embryo of 6 primary segments. Basal segment irregularly divided. FIGS. 13 and 14. Slender types. No irregular divisions in basal segments. All × 300.

In the later stages of development the writer has been unable to trace with any degree of certainty the original wall separating the basal and apical cells which Waldner in his drawings shows as sharply defined. As illustrated by figures 2–14, it is evident that in the material here studied there is no sharp delimitation, hence an exact statement as to the part contributed by each of these cells would be unwarranted. While no division figures could be found, the elongation of the apical cell as shown in figures 3, 8, and 12 furnishes strong evidence of apical growth, and finds frequent corroboration in the position of the nuclei as illustrated by the two uppermost cells in each of figures 7 and 11. Whether this apical growth may be supplemented by the occasional intercalary division of a primary segment is questionable. Cell *a* in figure 4 suggests such a possibility. The elongation of this cell together with the size of the nucleus makes it seem probable that such a division is about to take place.

While it is impossible to trace with absolute certainty all of the divisions undergone by the basal cell, a study of basal regions shows two distinct types of divisions (figs. 2–21). As illustrated by figures 3, 8, 9, 11, and 12, the basal cell divides irregularly, while in the embryos shown in figures 6, 7, 13, 14, and 15, if the basal cell has divided the divisions are regular, *i.e.*, brought about by walls parallel to that first formed. This irregularity or regularity expresses itself later in what might be termed two types of young sporophytes. The first of these, in which the lower portion is distinctly bulbous, is derived from the irregular type. The cells formed by these irregular divisions grow considerably in size and tend to round away from each other (figs. 16–17). Such embryos stand in sharp contrast to those of

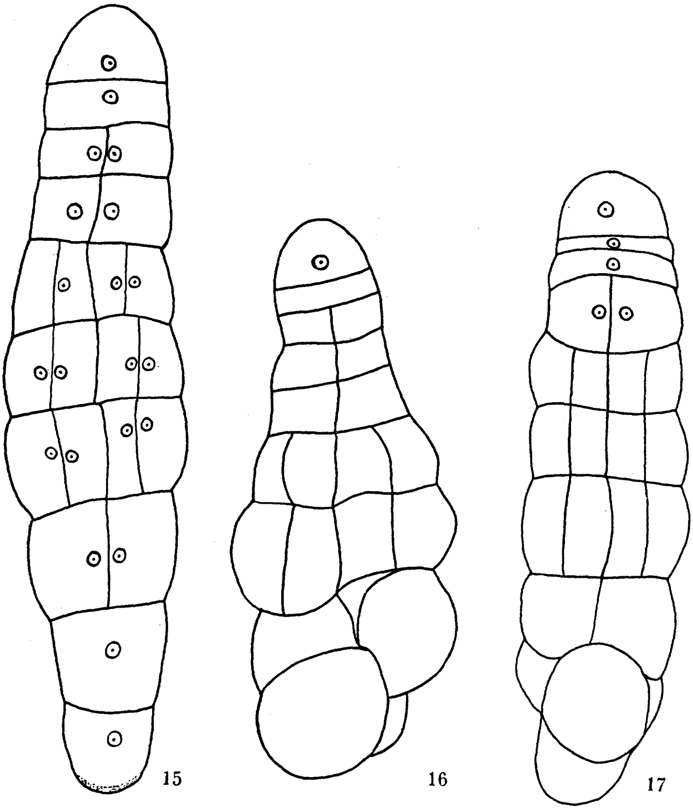

FIG. 15. Embryo showing 10 primary segments. Basal portion of sporophyte slender and without irregular divisions. FIG. 16. Bulbous type of young embryo. Cells of basal portion have strong tendency to round away from each other. FIG. 17. Embryo showing probably 9 primary segments. Basal portion bulbous. All × 300.

the second type in which the basal cells are regular and slender and remain so for some time, apparently serving as a distinct boring organ aiding the young sporophyte in digesting its way into the stalk of the archegonium (figs. 15, 18, 20, 21). Such a structure is somewhat suggestive of an inverted suspensor. Figures 22 and 23, sketched from living material, give

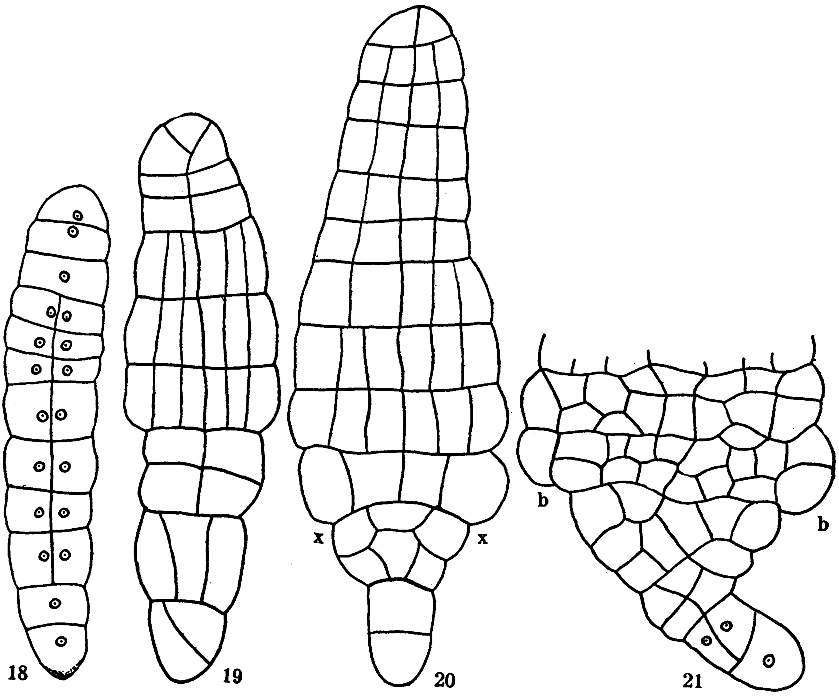

FIG. 18. Embryo showing 12 primary segments, the maximum number found in the material studied. The sporophyte is of the slender, regular type. FIGS. 19 and 20. Later stages of development. In the embryo shown in figure 20 the foot proper will develop above wall *x–x*. FIG. 21. Basal portion of young embryo at later stage than figure 20. The foot proper is beginning to develop along the region *b–b*. All × 180.

some idea of how quickly the young sporophyte bores its way out of the venter. In figure *22a*, the embryo has already begun to digest the cells of of the venter immediately below it. In figure *22b*, the embryo has worked its way entirely out of the venter and is embedded in the stalk of the archegonium. Figure 23 shows a still later stage in which the stalk of the archegonium has developed considerably in thickness, and illustrates the expansion of the basal portion of the young sporophyte to form the foot. It should be noted, however, that the immediate basal cells of the slender type do not form this expanded foot. In the embryo shown in figure 20, the foot will arise from the cells above the segment *x* — *x*. In figure 21 the expansion to form the foot proper can be observed at *b* — *b*.

An interesting situation is illustrated in figures 24–26. When the dissections were first begun, a large percentage of the young sporophytes were found to be disintegrating. This disintegration, in all the cases observed, begins with the apical cell and works downward. The cause

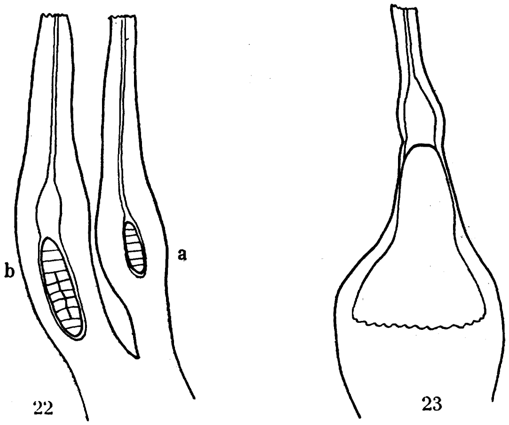

FIG. 22*a*. Young embryo beginning to digest the cells of the venter. FIG. 22*b*. The embryo has bored its way entirely out of the venter and lies embedded in the stalk of the archegonium. FIG. 23. Later stage showing the spreading of the foot. All × 60.

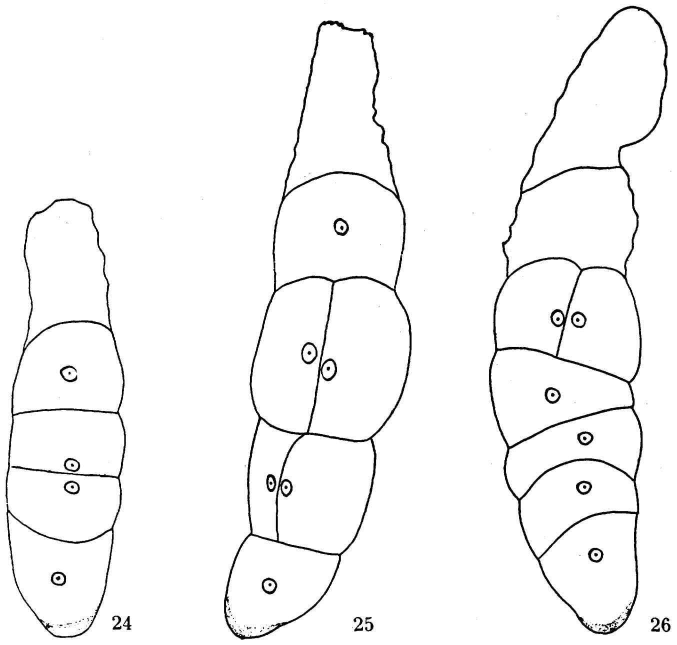

FIG. 24. Embryo of 5 cells. Apical cell has degenerated. FIG. 25. Older stage, apical cell degenerating. FIG. 26. Embryo of 7 primary segments. the two uppermost having degenerated. All × 300.

could not be discovered. No fungus could be observed on or about the archegonia in these particular cases. The cells which had not disintegrated were apparently normal in every respect. It was unquestionably similar observations which led Schimper to state that it is the lower part of the young embryo which finally produces the sporophyte, the upper part dying and being resorbed.

Summary

The main points of this paper may be summarized as follows:

1. The fertilized egg divides by a horizontal wall into two approximately equal cells. A filament of cells—6 or 7 in number—is usually formed before longitudinal divisions occur.
2. In the material studied the wall which separates the cells at the two-celled stage cannot be traced with certainty in the older stages, hence no exact statement can be made as to the contribution of each of these two cells in the development of the sporophyte.
3. It is reasonably certain that apical growth occurs.
4. The basal portion of the young sporophyte may have walls appearing in a regular or in an irregular order. As a result of the former process there is developed a long, slender type of young sporophyte; as a result of the latter a shorter, bulbous type.
5. The number of primary segments, *i.e.*, segments formed by walls transverse to the axis of the archegonium, has not been found to exceed twelve.
6. A considerable number of very young sporophytes show basipetal disintegration.

Conclusions

Much has been made of the striking character common to the Anthocerotales and the Sphagnales as contrasted with the remaining members of the Bryophyta—namely, the origin of the sporogenous tissue from the endothecium. The writer desires to point out the wide difference in early embryogeny. The general history in the Anthocerotales is the formation of an unequal quadrant, the two upper cells being somewhat larger than the basal ones. This stands in sharp contrast to the filament of six or seven cells produced in Sphagnum. An examination of the early embryogeny of the Bryophyta shows that the closest approach in this respect to the condition in Sphagnum is to be found among the Jungermanniales. Here a filament of three cells formed before the appearance of vertical walls is not uncommon.

If similarity in early embryogeny is significant in determining phylogeny, it must be evident that in this one respect Sphagnum shows a closer relationship to the Jungermanniales than to any other group of the Bryophyta

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